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ORIGINAL ARTICLE

Genome-wide identification, characterization of expansin gene family of banana and their expression pattern under various stresses

Suthanthiram Backiyarani[1] · **Chelliah Anuradha**[1] · **Raman Thangavelu**[1] · **Arumugam Chandrasekar**[1] · **Baratvaj Renganathan**[1] · **Parasuraman Subeshkumar**[1] · **Palaniappan Giribabu**[1] · **Muthusamy Muthusamy**[2] · **Subbaraya Uma**[1]

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Abstract

Expansin, a cell wall-modifying gene family, has been well characterized and its role in biotic and abiotic stress resistance has been proven in many monocots, but not yet studied in banana, a unique model crop. Banana is one of the staple food crops in developing countries and its production is highly influenced by various biotic and abiotic factors. Characterizing the expansin genes of the ancestor genome (*M. acuminata* and *M. balbisiana*) of present day cultivated banana will enlighten their role in growth and development, and stress responses. In the present study, 58 (MaEXPs) and 55 (MbaEXPs) putative expansin genes were identified in A and B genome, respectively, and were grouped in four subfamilies based on phylogenetic analysis. Gene structure and its duplications revealed that EXPA genes are highly conserved and are under negative selection whereas the presence of more number of introns in other subfamilies revealed that they are diversifying. Expression profiling of expansin genes showed a distinct expression pattern for biotic and abiotic stress conditions. This study revealed that among the expansin subfamilies, EXPAs contributed significantly towards stress-resistant mechanism. The differential expression of *MaEXPA18* and *MaEXPA26* under drought stress conditions in the contrasting cultivar suggested their role in drought-tolerant mechanism. Most of the *MaEXPA* genes are differentially expressed in the root lesion nematode contrasting cultivars which speculated that this expansin subfamily might be the susceptible factor. The downregulation of *MaEXPLA6* in resistant cultivar during Sigatoka leaf spot infection suggested that by suppressing this gene, resistance may be enhanced in susceptible cultivar. Further, in-depth studies of these genes will lead to gain insight into their role in various stress conditions in banana.

Keywords A and B genome · Banana · Biotic and abiotic stresses · Expansin · Gene expression

Abbreviations

EXP	Expansin
qRT-PCR	Quantitative real-time polymerase chain reaction
FAO	Food and Agriculture Organization
HMM	Hidden Markov model
PPI	Protein–protein interaction
MEME	Multiple Em for motif elucidation
MEGA	Molecular evolutionary genetics analysis
MeJA	Methyl jasmonate

Introduction

Banana and plantain represent a significant source of economic growth, income, food security, and nutrition and around 99% of production are from developing countries (FAO 2020). The banana production is greatly affected by biotic (corm weevil, root lesion and root knot nematodes, Fusarium and bacterial wilt, bunchy top virus disease, etc.) and abiotic stresses (salinity, heat, drought) which affects the livelihood of smallholding banana farmers (Nansamba et al. 2020). Thus, for sustainable banana production, the

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Suthanthiram Backiyarani, Chelliah Anuradha and Arumugam chandrasekar have contributed equally to this work.

✉ Suthanthiram Backiyarani
backiyarani@gmail.com; Backiyarani.S@icar.gov.in

[1] ICAR-National Research Centre for Banana, Thogamalai Road, Thayanur Post, Tiruchchirappalli, Tamil Nadu 620 102, India

[2] Department of Agricultural Biotechnology, National Institute of Agricultural Sciences (NAS), RDA, Jeonju 54874, Korea

cultivation of resistant/tolerant accessions becomes the key factor (Blomme et al. 2011). Incorporation of resistance, without co-inheritance of undesirable genes through conventional breeding approach is complex owing to its poor seed setting nature. This co-inheritance of undesirable genes can be avoided by implementing the gene manipulation techniques either through over expression or knockdown of target genes with functions associated with resistance/tolerance or susceptibility phenotypes (Datta 2013). The success of the genetic engineering/genome-editing techniques depends on identifying the target genes that need to be manipulated. The mechanism of tolerance/resistance in bananas has been well studied for various abiotic and biotic stresses (Wang et al. 2012; Li et al. 2013; Backiyarani et al. 2014; Saravanakumar et al. 2016; Muthusamy et al. 2016), and there is clear evidence of involvement of genes pertaining to signaling perception and transduction, transcription factors, disease resistant proteins, plant hormones and cell wall organization. Plant cell wall not only provides a structural framework for plant growth; but also act as a barrier to protect the cells in response to biotic and abiotic stresses (Tucker and Koltunow 2014) through remodeling and disassembly of the cell wall (Marowa et al. 2016). In banana, it has been evidenced that cell wall-modifying genes are associated with biotic stress resistance (Van den berg et al. 2007) and drought tolerance (Muthusamy et al. 2016; Cheng et al. 2016; Wang et al. 2017).

These cell wall modification are achieved through the action of various proteins, of which expansin, a structural protein, is secreted into the cell wall space and plays a major role in expansion (Fukuda 2014). Cosgrove (2000) and Bashline et al. (2014) reported that expansin act as cell wall loosening agents and like a zipper, breaks the hydrogen bonds between cellulose micro fibrils and matrix polysaccharides. This expansin mediated cell wall modification is associated with environmental stress tolerance such as drought (Zhao et al. 2011; Li et al. 2011b) heat (Zhao et al. 2011), salt (Lüet al. 2013; Zorbet al. 2015), and oxidative stress tolerance (Han et al. 2017). Similarly, Abuqamar et al. (2013) evidenced that tolerant level has been enhanced for the necrotrophic fungi through suppressing the expansin genes and up regulation of expansin gene was observed during cyst nematode infestation in tomato (Fudaliet al. 2008) and soybean roots (Ithal et al. 2007; Klink et al. 2007). The differential expression of expansin genes in different tissues such as leaf (Pien et al. 2001a, b), stem (Santiago et al. 2018), root (Lee et al. 2003), pollen (Pezzottiet al. 2002), fruit (Brummell et al. 1999a, b), and seed (Yan et al. 2014) revealed that they have diverse functions and differential expression in various tissues, development stages, and stress conditions. In banana, the whole-genome sequencing of the ancestors of A and B genome have been completed by D'Hont et al. (2012) and Davey et al. (2013), and the comparative genome analysis of banana with maize, rice, sorghum, date palm, *Brachypodium* and *Arabidopsis* proteomes revealed that enzymes of cell wall biosynthesis of Musa are forming a specific clusters (D'Hont et al. 2012). This emphasized that in-depth study on expansin, a cell wall protein, is warranted to understand their role under various physiological stages of banana. This emphasized that a more comprehensive understanding of the expansin classes and their possible differential expression patterns in banana tissues and stress conditions are essential and useful for dissecting their role in bananas. This can be achieved through comparative analysis of gene families from the expression profile of the contrasting cultivars under challenged and unchallenged conditions (Kaliyappan et al. 2016). To date, the role of banana expansins has been studied only for fruit ripening (Trivedi and Nath 2004; Asha et al. 2007; Asif et al. 2014) and their role on biotic and abiotic stress resistance are yet to be studied. Thus, the present study has been carried out for a systemic analysis on expansins in A and B genome of *Musa*, the ancestors of the present day commercial cultivars, through genome-wide identification, characterization, and their expression in the contrasting cultivars during biotic (*Pseudocercospora eumusae*, *Pratylenchus coffeae*) and drought stresses.

Materials and methods

Identification of expansin family members in banana

The nucleotide and protein sequences of expansin genes of A and B genome were downloaded from the Banana genome hub database (https://banana-genome-hub.southgreen.fr/). The genome IDs of expansins were arranged according to their location in chromosomes from Chr01 to Chr11. Expansin IDs were assigned for each subfamily as EXPA, EXPB, EXPLA, and EXPLB suffixed with Ma and Mb for A and B genomes, respectively (Supplementary file 1). The expansin sequences of the model crop, *Arabidopsis thaliana*, and *Oryza sativa* were obtained from Phytozome v12.1 (https://phytozome.jgi.doe.gov/pz/portal.html) and used as query sequences to perform the blast searches against A and B genome with a 1×10^{-5} cutoff *e* value. Protein sequences of putative expansins were examined by PFAM (http://pfam.xfam.org/) to confirm the existence of the conserved domains (DPBB_1 domain and Pollen_allerg_1 domain) and candidate genes not having the characteristic domains were discarded for further study. Hidden Markov Model (HMM) with PFAM numbers PF03330 and PF01357 were used to search putative expansin genes in the protein dataset using HMMSEARCH with a threshold of *e* values $< 10^{-5}$ (Finn et al. 2010). The molecular weight (MW) and isoelectric point (pI) were acquired from the ExPaSy (https://web.expasy.org/compute_pi/) for each protein sequence. Subcellular localization of the expansin proteins was predicted by online software WoLF PSORT II (https://www.genscript.com/wolf-psort.html?src=leftbar).

Phylogenetic tree construction

Multiple sequence alignment was done to explore the evolutionary relationships of expansins between *Musa* (A, B genome), rice, and *Arabidopsis* with default parameters using MUSCLE v.3.8.31 (Larkin et al. 2007). MEGA10.0 was performed to construct a maximum likelihood (ML) phylogenetic tree using all sites with bootstrap analysis (1000 replicates) (Kumar et al. 2018).

Gene structure, cis-regulatory elements and genomic distribution of expansin genes in banana

The structure (exon–intron) of the expansin genes was drawn by the Biosequence Structure Illustrator program of the TBtools software v. 1.077 (Chen et al. 2020). MEME tool was used to identify the conserved motifs (http://meme-suite.org/tools/meme). TBtools was used for mapping the expansin genes on the *Musa* A and B genome. Quick MCScanX Wrapper program of TBtools was used to identify the tandem and segmental duplication gene pairs. Upstream sequences (2 kb) of each expansin genes were analyzed to identify cis-regulatory elements using Plant CARE (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/).

Synteny and gene duplication analysis

Duplication events of the expansins were analyzed using MCScanX (Wang et al. 2012). Advanced Circos was used to create collinear analysis diagrams for both *Musa* A and B genome (Chen et al. 2020). Multiple synteny plot was drawn between *Musa* A, B genome with *A. thaliana* and *O. sativa* using TBtools.

Ka/Ks analysis and estimated divergence time for the duplicated *Musa* expansins

Gene duplication events were analyzed by calculating non-synonymous substitution rate and synonymous replacement rate using PAML program (Yn00 package) (Xu and Yang 2013; Nei and Gojobori 1986). As Ks of duplication genes are expected to be similar over time in a molecular clock (Shiu et al. 2004), Ks values for each gene pair were used to calculate the approximate date of the duplication time (T) (million years ago, Mya) using the formula: $T = \mathrm{Ks}/2\lambda \times 10^{-6}$ where λ = clock-like substitution rate (Lynch and Conery 2000) and λ for banana = 4.5×10^{-9}) (Lescot et al. 2008).

Expression analysis of expansins

The differential expression value (log2 fold change) of expansins during *P. eumusae*, *P. coffeae*, and drought stress conditions in the respective contrasting cultivars were retrieved from the database maintained at ICAR-NRCB (http://nrcb.res.in/nrcbbio/about.html). Significant log2 fold change values of the contrasting expressed expansins were used to draw a heat map by TBtools.

Plant materials and stress treatments

The pot cultured plants of *P. eumusae*-resistant (cv. Manoranjitham, AAA) and -susceptible (cv. Grand Nain, AAA) cultivars were inoculated by spraying *P. eumusae* spores on both surfaces of leaves as per the protocol followed by Saravanakumar et al. (2016). The suckers of *P. coffeae*-resistant (YKM 5, AAA) and -susceptible (cv. Nendran, AAB) cultivars were pared and treated with fungicides, nematicides, and pot cultured. Four weeks after planting, mixed life stages of root lesion nematode (*P. coffeae*) were inoculated by following the methodology developed by De Schutter et al. (2001). Roots were collected at 0 and fifth day after inoculation. Uniform size suckers of drought-tolerant (cv. Saba, ABB) and -susceptible (cv. Grand Nain, AAA) cultivars were pot cultured. Five months old plants were subjected to water-deficit stress (Ravi and Uma 2011) and leaf samples were collected at 0 and 20 days. Leaf and root samples collected at different time intervals under different stresses were snap-frozen in liquid nitrogen and stored at − 80 °C for further use.

Quantitative real-time PCR (qRT-PCR)

Total RNA was isolated from challenged and unchallenged contrasting cultivars for various stresses independently using Sigma RNA isolation kit (Sigma, USA) following manufactures protocol. One microgram of RNA of each sample was used for cDNA synthesis (cDNA synthesis kit, Thermo Scientific, USA). Synthesized cDNA was diluted (1:10) with nuclease free water and used as a template. Specific gene primers were designed using *Musa acuminata* ssp. *malaccensis* (DH Pahang) sequences by the Primer3Plus tool which is used for expression studies. The expression of unchallenged resistant and susceptible cultivars under each stress was considered as a control to calculate the fold change in their respective challenged cultivars. Ribosomal protein S2 (RPS) was used as the internal control. The total experiment was conducted in the Roche LightCycler®

480 System with LightCycler® 480 Software Version 2.0 (Table S3).

Interaction network of expansin proteins

Protein–protein interaction (PPI) was studied using STRING v11.0 (Szklarczyk et al. 2019) for expansin genes of A and B genome independently. The PPI network was constructed using the *A. thaliana* as a reference. The minimum required interaction score parameters were set at the medium confidence level.

Results

Identification of banana expansin genes

A total of 58 and 55 expansin gene sequences of *M. acuminate* ssp. *malaccensis* (DH-Pahang) and *M. balbisiana* (DH-PKW), respectively, were retrieved from the banana genome hub (Droc, 2013). The subfamilies of expansin genes (EXPA, EXPB, EXLA, and EXLB) were identified based on the conserved domains, double-psi β-barrel (DPBB) and the β-sandwich (D2 ± pollen allergen domain) and found that maximum genes belong to the EXPA subfamily (36 and 33) followed by EXPB (12, 15), EXPLA (6, 6) and EXPLB (3, 1) in A and B genome, respectively. Of which only 83 and 64% of the genes present in A and B genome, respectively, had signal peptides. Except few, all the members of EXPA and EXPLA had a pI value above 7.0. However, the pI values of all EXPBs and EXPLBs were below 7.0, except for six members (Supplementary file 2).

Gene structure and phylogenetic analysis

The structure of expansin genes revealed that they are diverse among and between the members of the subfamilies (Fig. 1a, b) which might be due to loss or gain of introns. In A genome, 30 genes had 3 exons, 14 had 4 exons, 8 had 5 exons, 5 had 2 exons, and 1 (*MaEXPB2*) had only 1 exon (Fig. 1a), while 1 to 6 exons were found in expansin genes of B genome. It was observed that 2 had 6 exons, 5 had 5 exons, 11 had 4 exons, 25 had 3 exons, 10 had 2 exons, and 1 (*MbaEXPB3*) had only 1 exon (Fig. 1b). The EXPA members contained mostly three exons except for a few genes, but all EXPB, EXLA, and EXLB genes contained more than three exons in both the genomes.

In total, 20 conserved motifs were identified in banana expansin genes (Fig. 1a, b) (Supplementary file 3). Among them, motif 4, 6, 7, 14 and 3, 4, 6, 10 were highly conserved in all the subfamilies in both A and B genome, respectively. In the EXPA group, motifs 0, 3, 4, 6, 9, 15 constitute the DBPP domain, while motifs 1, 5, 7 constitute the Pollen_allerg domain. Motifs 3, 6, 8 are commonly present in EXPB, EXPLA, and EXPLB subfamilies whereas motif 0 is common to EXPB and EXLA alone and constitute the DBPP domain, while motifs 5, 10, 12 are common to EXPB and EXPLB whereas motifs 5, 11, 16 are present in EXPLA and constitute the Pollen_allerg domain in A genome. In the case of B genome, motifs 0, 2, 4, 6, and 12 constitute the DBPP domain, while motifs 1, 5, 7 constitute the Pollen_allerg domain in EXPA. The EXPB and EXLA had motifs 0, 2, 4, 15 while, EXLB had motifs 2,4,13 and constitute the DBPP domain, whereas motifs 5, 8, 11, 16, motifs 8, 10, 17 and motifs 8, 11, 15, respectively, constitute the Pollen_allerg domain. Phylogenetic analysis grouped these expansin genes into above-mentioned four major classes (Fig. 2) and found that EXPA was the largest class in both the genomes.

Chromosomal location and synteny analysis

The expansin genes were unevenly mapped on 11 chromosomes and the distribution was almost similar in both the genomes. Chromosome 02 had 13 expansins in both the genome, while chromosome 03 in A genome and 08 in both the genomes had no expansin genes (Fig. 3a, b). The collinear relationship of *MaEXP* and *MbaEXP* was studied and the results indicated that the expansion of the expansin gene family was due to tandem, segmental or whole-genome duplication (WGD) (Fig. 4a, b). Most of the tandem and segmental duplication have occurred in chr 02 of both the genomes. Synteny relationship of expansin genes was studied to understand the evolutionary events that had taken place among the orthologous from *O. sativa* (56 genes), *A. thaliana* (36 genes), and *Musa* (A and B genome). Most of expansin genes showed a one-to-one corresponding relationship between A and B genome and with *O. sativa* than with *A. thaliana* (Fig. 5) (Table S2).

Ka/Ks analysis and estimated divergence time for the duplicated expansins

A maximum number of paralogues was observed for EXPA (A genome 90%, B genome 66%) followed by EXPB (A genome 10%, B genome 34%), whereas no paralogues were observed for EXPLA and EXPLB subfamilies. The paralogues harboring similar gene structures had a more similar function in both the genome (Supplementary file 4). For example, *MaEXPA16* and 14 having similar exon and intron structures showed similar putative biological function (C: extracellular region; C: cell wall; P: plant-type cell wall organization; C: integral component of membrane) (Jinet et al. 2020). Variation in gene structure and function between paralogues has been suggested to be a consequence of the evolutionary pressure that favors the retention or loss of the mutated alleles from a population (Lan et al. 2009).

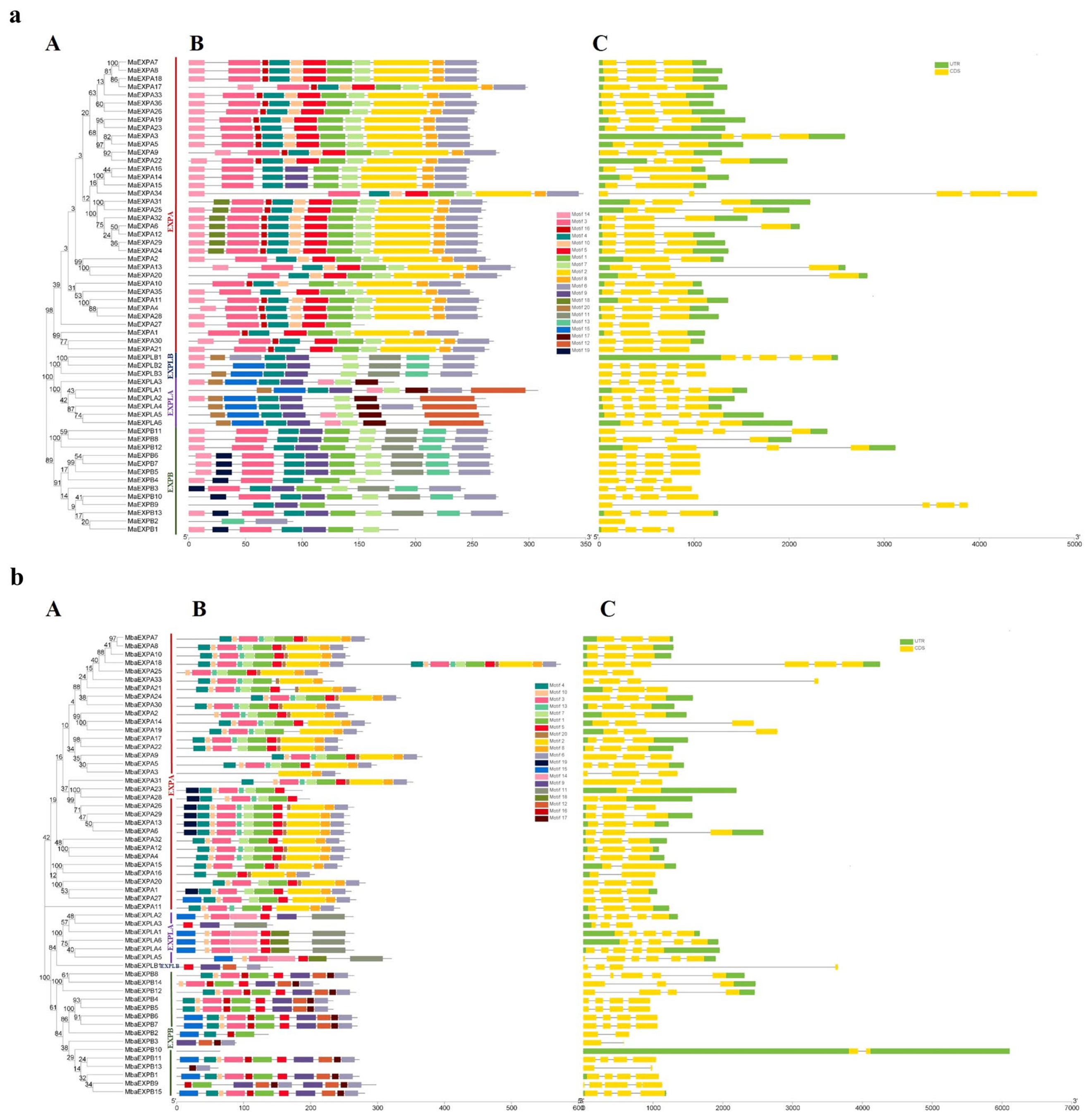


Fig. 1 **a** Phylogenetic relationship, motif compositions and gene structure of expansin genes in Musa A genome. **A** Phylogenetic relationships of 58 expansins in Musa A genome, They are classified in four groups: α-expansin (EXPA), β-expansin (EXPB), expansin-like A (EXLA) and expansin-like B (EXLB); **B** different motif compositions of expansins in Musa A genome. The conserved motifs are represented by boxes with different colors. **C** Gene structure organization of expansin genes of Musa A genome. **b** Phylogenetic relationship, motif compositions and gene structure of expansin genes in Musa B genome. **A** Phylogenetic relationships of 55 expansins in Musa B genome, They are classified in four groups: α-expansin (EXPA), β-expansin (EXPB), expansin-like A (EXLA) and expansin-like B (EXLB); **B** different motif compositions of expansins in Musa B genome. The conserved motifs are represented by boxes with different colors. **C** Gene structure organization of expansin genes of Musa B genome

Analysis of selection pressure among the duplicated *MaEXP* and *MbEXP* gene pairs revealed that 17 duplicated pairs of both the genome were under purifying or negative selection; Three of A genome and one of B genome duplicated pairs resulting from the positive selection or accelerated evolution and 3 neutral selection in B genome (Supplementary file 4).

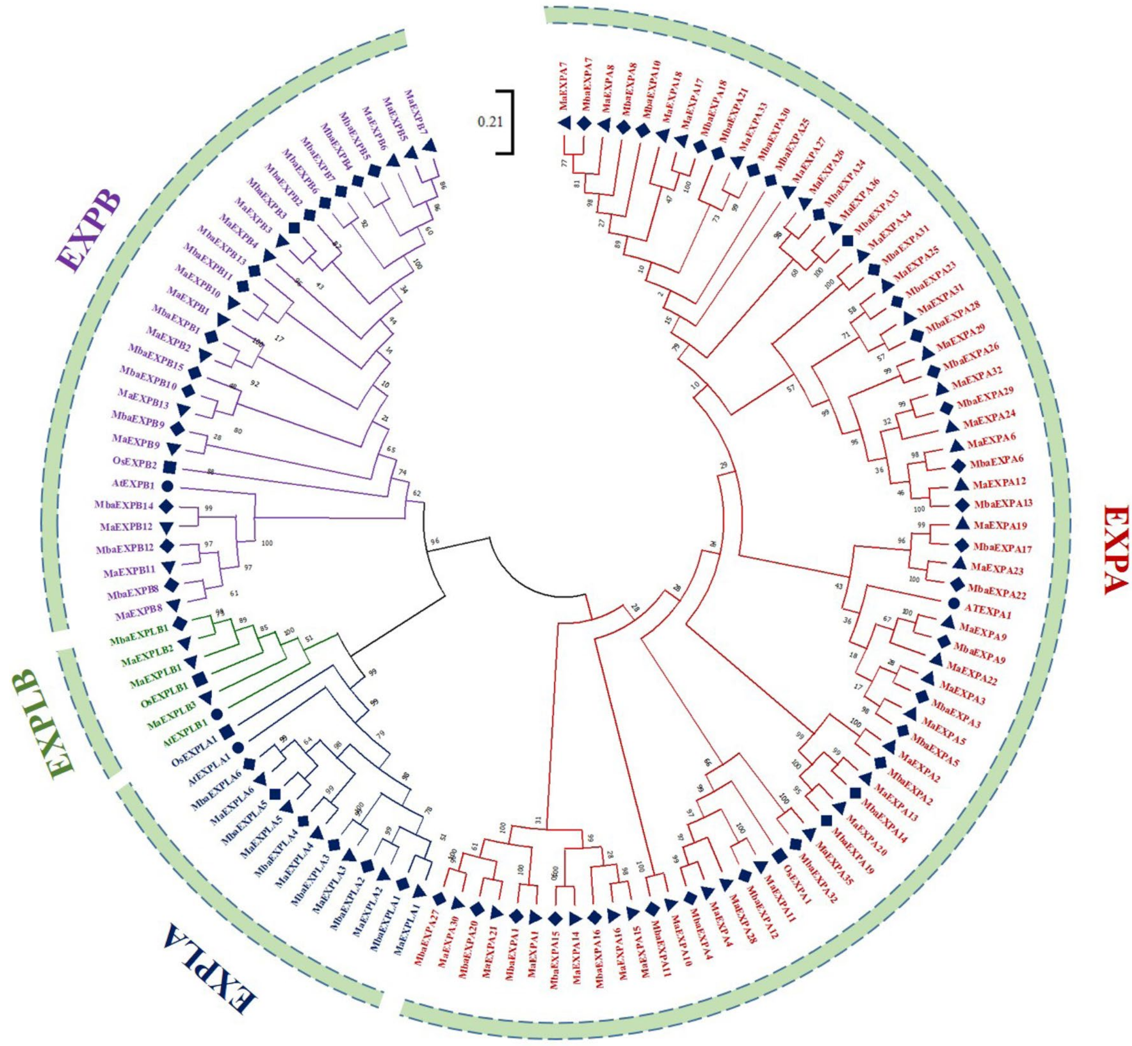


Fig. 2 Phylogenetic tree of expansins from Musa A & B genome, *Arabidopsis* and *Oryza*. MEGA10.0 was used to construct a Maximum Likelihood phylogenetic tree with 1000 bootstrap replications. Triangles, circles, squares and diamond shapes represent the expansins of Musa A, B, rice, *Arabidopsis*, respectively. Bootstrap values are shown on the tree

The duplication events of *MaEXP* and *MbEXP* paralogues are suggested to have occurred between 1.08 and 40.59 million years ago (Mya) in A genome and 1.07 to 122.94 Mya in the case of B genome, respectively (Supplementary file 4). Among the duplication events, 6 and 7 of the 20 and 21 pairs are suggested to be more recently duplicated, of which, the paralogues of EXPB subfamily members were recently evolved in both the genomes but found more in B genome.

Cis-elements

Cis-elements in the expansin promoter were identified using the PlantCARE database (Fig. 6a, b), (Supplementary file 5). Three types of cis-elements related to development, hormone, and abiotic stresses were identified. Cis-elements related to development include light-response, metabolism regulation, and meristem expression; hormone stress include methyl jasmonate (MeJA), abscisic acid (ABA)-responsive relate element (ABRE), gibberellin (GA)-responsive and auxin-responsive; abiotic stresses include anoxic-specific inducible element GC-motif, drought-inducible cis-element MBS and low-temperature responsive (LTR) were identified. Among these, MeJA, ABRE and drought-responsive cis-elements were abundant. A total of 51, 47 MeJA; 52, 48 ABREs; and 35, 37 drought-responsive elements were found in the promoter regions of both the genomes of banana, respectively. Among them *MaEXPA7* had 12 ABREs response elements, *MaEXPA7* and *MaEXPA10* had 7 MeJA stress response elements, and *MaEXPA22*, *MaEXPA23*, and *MaEXPB8* had a maximum of three drought-responsive elements in A genome. *MbaEXPB*8 had 12 ABREs, *MbaEXPA11* had 9MeJA stress response elements and

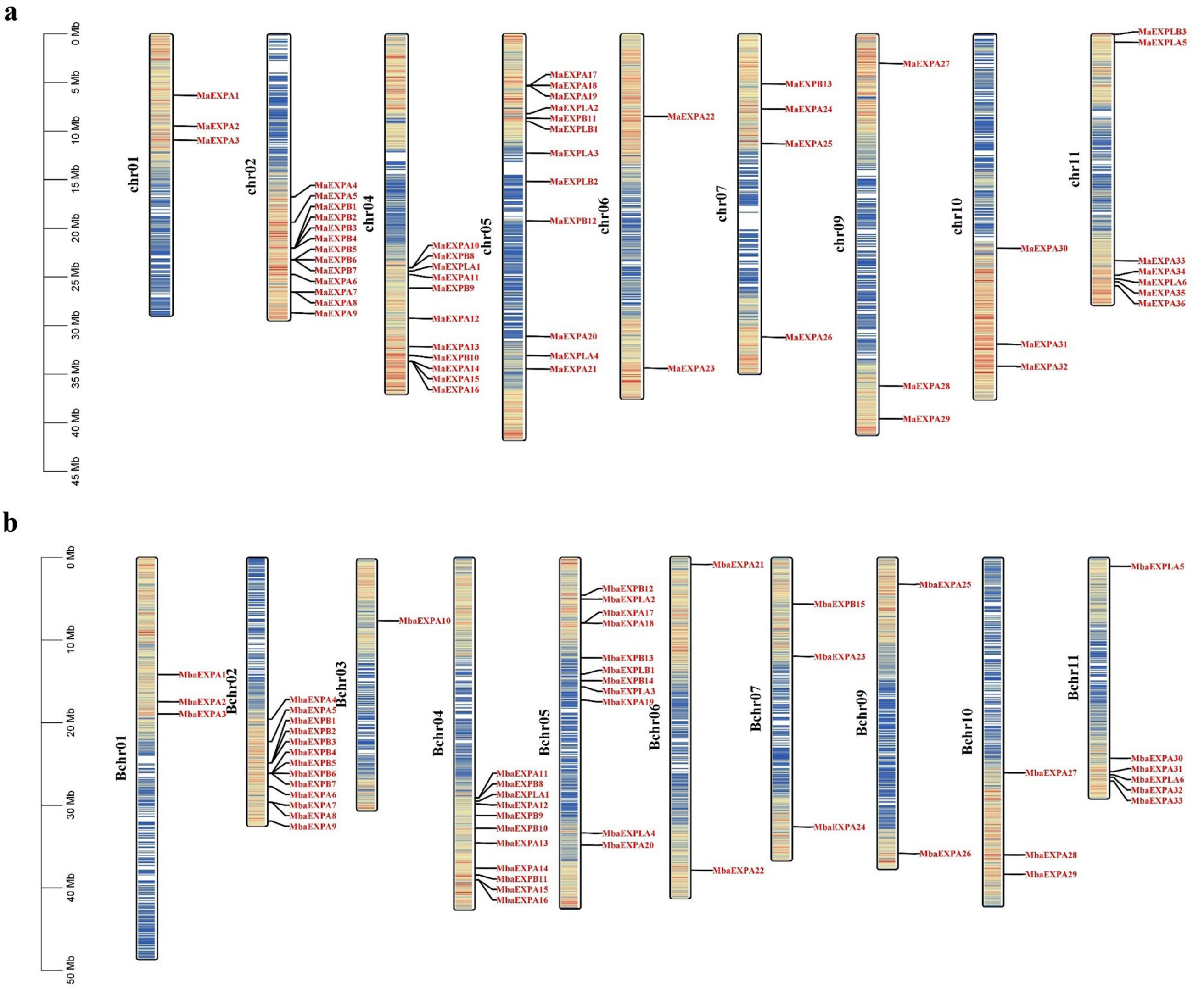


Fig. 3 **a** Distribution of expansin genes on chromosomes in Musa A genome. The gene density is displayed in the form of heatmaps on the chromosomes, high and low densities are represented by red and blue. **b** Distribution of expansin genes on chromosomes in Musa B genome. The gene density is displayed in the form of heatmaps on the chromosomes, high and low densities are represented by red and blue

MbaEXPA22, *MbaEXPB15*, and *MbaEXPLA2* had three drought-responsive elements in B genome (Fig. 7a, b).

Differential expression of expansins under various stresses and validation through qRT-PCR analysis

The expression profile of expansins was analyzed from the challenged and unchallenged transcriptome data of resistant and susceptible cultivars under biotic and abiotic stress conditions (Fig. 8). It is interesting to note that 27.5% of genes (16 numbers) were not expressed in the samples (root/leaf) taken for this study. Among non-expressed genes in each subfamily, 70% belong to EXPB followed by EXPLB (66%). Out of 72.5% of expressed genes, 13 (*MaEXPA2*, *MaEXPA4*, *MaEXPA8*, *MaEXPA10*, *MaEXPA11*, *MaEXPA14*, *MaEXPA15*, *MaEXPA21*, *MaEXPA23*, *MaEXPA28*, *MaEXPA32*, *MaEXPA35*, *MaEXPB8*) were expressed only in root whereas one (*MaEXPA33*) was expressed only in leaf tissue (Supplementary file 6).

Among the expressed expansin genes, a maximum number of expansins were differentially expressed under nematode infection (43%) followed by drought (28%) and Sigatoka infection (24%). None of the *MaEXPLB* genes was significantly differentially expressed in the contrasting cultivars for all the stresses except MaEXPLB1 which was upregulated 3.57-fold upon challenge with Sigatoka in the susceptible cultivar. While maximum members of *MaEXPLA* were significantly differentially expressed in all the contrasting cultivars for all the stresses. In general, under drought, more genes were downregulated in susceptible

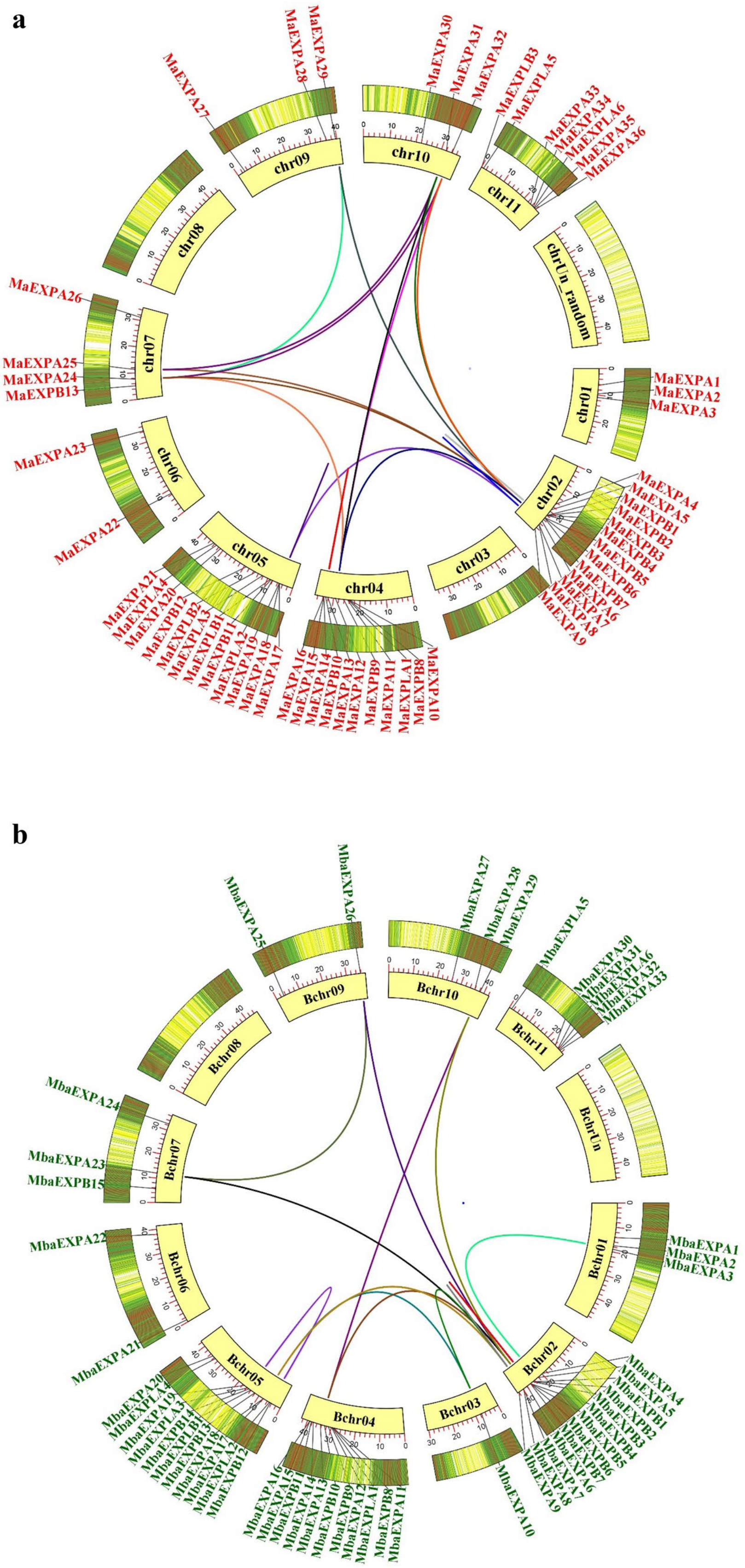


Fig. 4 **a** Collinearity mapping of expansin genes in Musa A genome. Different chromosomes are shown in yellow color. The gene density is displayed in the form of histogram. The inner colored lines represent the collinearity relationships of EXPA, EXPB and EXPLA subfamilies, respectively. A total of 13 pairs of Tandem and 19 pairs of segmented duplication genes were detected in the Musa A genome. **b** Collinearity mapping of expansin genes in Musa B genome. Different chromosomes are shown in yellow color. The gene density is displayed in the form of histogram. The inner colored lines represent the collinearity relationships of EXPA, EXPB and EXPLA subfamilies, respectively. A total of 16 pairs of Tandem and 14 pairs of segmented duplication genes were detected in the Musa B genome

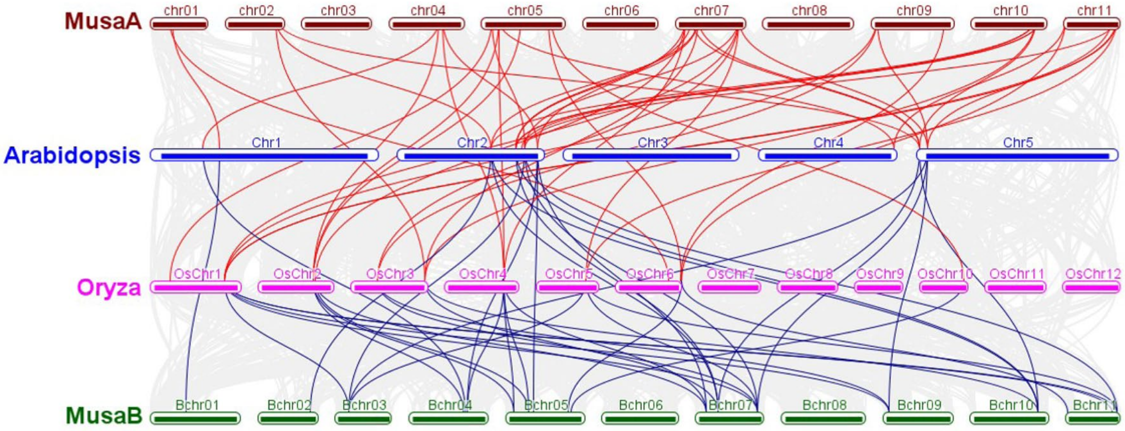


Fig. 5 Synteny analysis of expansin genes between Musa A genome, Musa B genome, *Arabidopsis* and *Oryza*. The gray lines in the background indicate the collinear blocks within Musa A, B and *Arabidopsis*, *Oryza* genomes, while the blue and red lines highlight the syntenic expansin gene pairs

(62%) compared to tolerant cultivar (46%). Among the 13 members of *MaEXPB*, only one (*MaEXPB13*) was highly upregulated in tolerant cultivar whereas no variation was observed in the susceptible cultivar upon drought.

Among the members of *MaEXPLB* and *MaEXPB* subfamilies, *MaEXPB8* alone showed > twofold downregulation in resistant cultivar upon nematode infection. This speculated that *MaEXPB8* may play a major role in nematode resistance. Three members of *MaEXPLA* subfamily (*MaEXPLA4,-5,-6*) were significantly upregulated only in a susceptible cultivar with > 1.5-fold whereas no variation was observed in resistant cultivar. This revealed that MaEXPLA members might be the susceptible factors as it favors nematodes by loosening the host cell and facilitates easy feeding. Similarly out of 20 members of *MaEXPA* subfamily, 50% of the members were significantly downregulated (> 1.5-fold) in resistant, whereas in susceptible cultivar except for *MaEXPA5* and -3, all other members were either upregulated or no variation in the expression.

Eight expansin genes were selected based on RNA-seq data and validated through qRT-PCR in the contrasting cultivars for each stress (Fig. 9). *MaEXPA*26 and *MaEXPB13* were differentially expressed in the contrasting cultivars upon drought stress. Most of the *MaEXPs* showed significant downregulation in resistant cultivar during *P. eumusae* infection. qRT-PCR data for nematode stress are in concordance with transcriptome data, and three genes, *MaEXPA*36, *MaEXPLA1*, and *MaEXPLA6* showed significant downregulation upon *P. coffeae* infection in resistant cultivar.

Interaction network of expansin proteins

The interaction network of the expansin proteins was constructed based on the interaction relationship of the homologous expansins proteins in *Arabidopsis* and this will help in understanding the biological phenomena in which expansins are involved in banana. The banana expansin proteins corresponded with the *Arabidopsis* expansin proteins are listed below them (Fig. 10a, b). The result showed that EXPA7 and EXPA18 from both the genomes were predicted as the core nodes in the network and interact with other proteins such as RHS12, PRP3, RHS19, RHS13, and MOP10, which suggested that they might participate in diverse functions by interacting with other proteins.

Discussion

Expansins participate in pH-dependent cell wall loosening during cell growth and are involved in plant growth, development and responses to abiotic and biotic stresses (Chen et al 2020) as shown in previous studies (Table S4). Among monocots, expansin genes were characterized in rice (Shin et al. 2005), wheat (Han et al. 2015), maize (Wu et al. 2001), and sugarcane (Santiago et al. 2018) but detailed studies on other monocots are warranted. Expansin superfamilies in banana are largely unexplored. Being a model crop for polyploidy and parthenocarpy, identification and characterization of genes in banana is paramount important which can be achieved with the availability of whole-genome sequencing of A and B genome (D'Hont et al. 2012; Davey et al. 2013). In this study, we performed a comprehensive analysis with both A and B genomes, which constitute all edible bananas, for the identification of expansin gene groups through in silico analyses. Further to gain more insight into their biological functions, the expression profiling of *MusaEXPs* (*MEXPs*) under drought, Sigatoka and nematode stresses were analyzed. In addition, key domains, promoter motifs, their evolutionary dynamics and structural syntenies were identified.

Herein, we identified 58 and 55 EXPs in *M. acuminata* and *M. balbisiana*, respectively, which are higher than rice, maize, sugarcane and this may be due to lineage specific duplication either by tandem and segmental duplication or transposition (Santiago et al. 2018; Han et al. 2019). In bananas, the presence of all the four subfamilies of expansin in banana indicated that this gene has emerged before the differentiation of the plant species. Though the expansin members of the same subfamily had similar properties, the significant difference at sequence level observed among the subfamilies revealed that expansin genes adapt to functional requirements by changing their properties (Han et al. 2019). Further, the presence of more members in the EXPA subfamily revealed their expansion and its function in growth and development (Lv et al. 2020) and under various stresses (Santiago et al. 2018). The intron–exon structure and motif composition were similar within the expansin subfamily suggesting that the genes belonging to the same subfamily are highly conserved, confirming their close evolutionary relationships (Han et al. 2019; Lv et al. 2020). The structure of expansin genes varies within the subfamily due to intron loss/gain events but the basic genetic structure is a 3-exon/2-intron pattern and similar results have also been reported in the case of tomato expansins (Lu et al. 2016). Insertion of introns might have occurred due to a type of transposable element which had splice sites or by the duplication of exonic sequences which had a splice site or due to mutate introns of non-classical types which probably do behave as self-inserting elements (Rogers 1990). The presence of

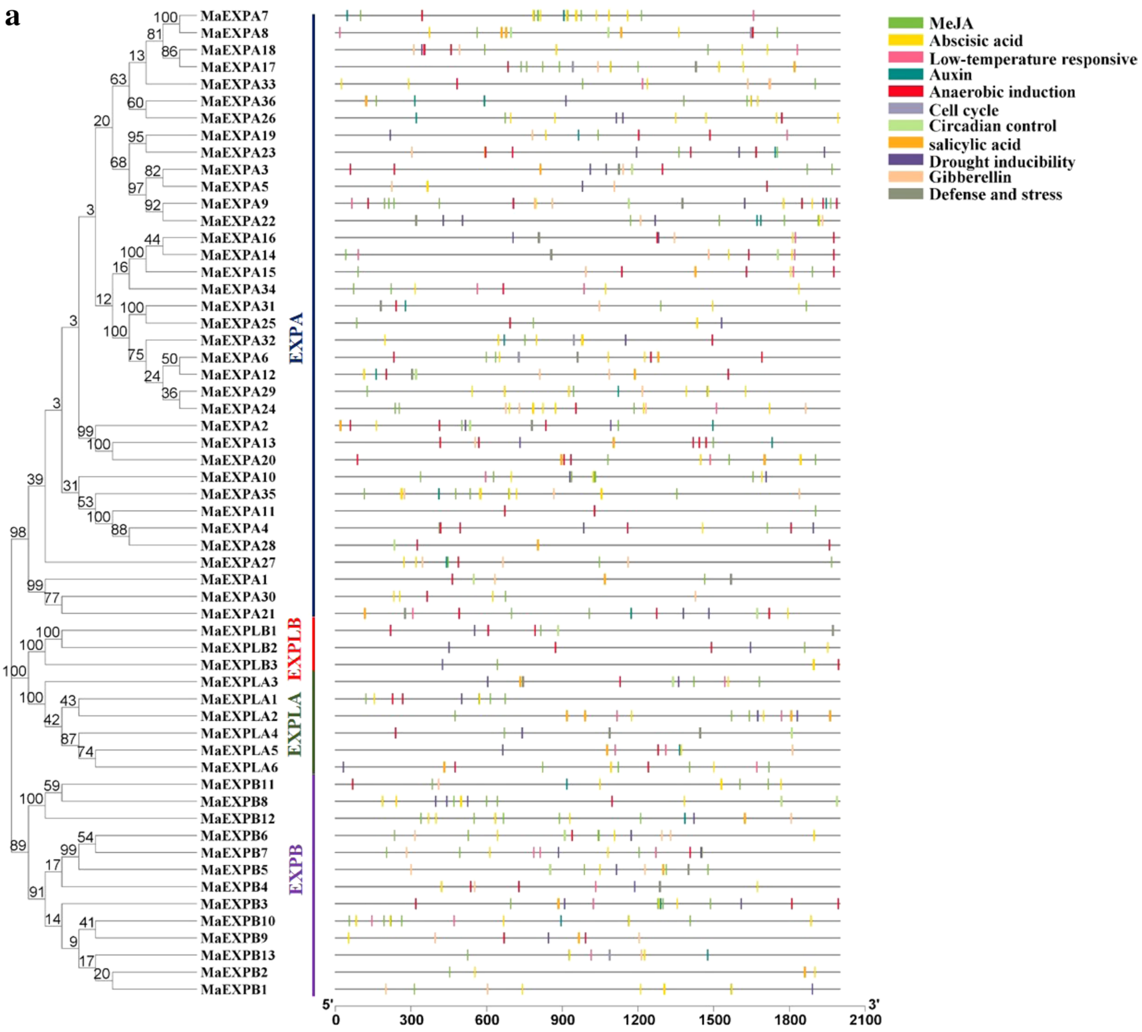
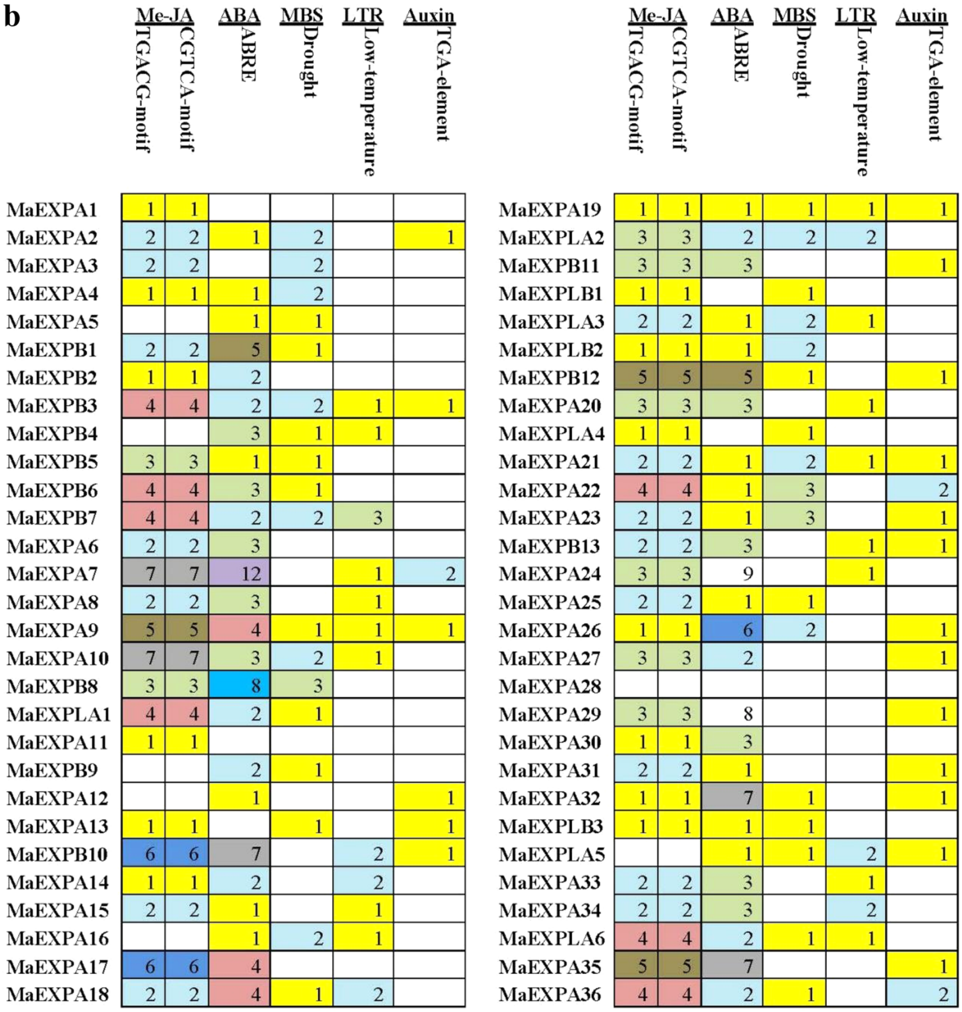


Fig. 6 **a** Predicted cis-elements of expansin gene promotors in Musa A genome. Promoter regions 2000 bp upstream of 58 EXPs analyzed by PlantCARE. Different-colored rectangles represented different cis-elements, and anaerobic induction response elements are highlighted in red ellipses. **b** The number of promoter elements in the MaEXPs' promoter regions. Five major cis-elements of MaEXPs are indicated by different-colored boxes with numbers



	Me-JA		ABA	MBS	LTR	Auxin
	TGACG-motif	CGTCA-motif	ABRE	Drought	Low-temperature	TGA-element
MaEXPA1	1	1				
MaEXPA2	2	2	1	2		1
MaEXPA3	2	2		2		
MaEXPA4	1	1	1	2		
MaEXPA5			1	1		
MaEXPB1	2	2	5	1		
MaEXPB2	1	1	2			
MaEXPB3	4	4	2	2	1	1
MaEXPB4			3	1	1	
MaEXPB5	3	3	1	1		
MaEXPB6	4	4	3	1		
MaEXPB7	4	4	2	2	3	
MaEXPA6	2	2	3			
MaEXPA7	7	7	12		1	2
MaEXPA8	2	2	3		1	
MaEXPA9	5	5	4	1	1	1
MaEXPA10	7	7	3	2	1	
MaEXPB8	3	3	8	3		
MaEXPLA1	4	4	2	1		
MaEXPA11	1	1				
MaEXPB9			2	1		
MaEXPA12			1			1
MaEXPA13	1	1		1		1
MaEXPB10	6	6	7		2	1
MaEXPA14	1	1	2		2	
MaEXPA15	2	2	1		1	
MaEXPA16			1	2	1	
MaEXPA17	6	6	4			
MaEXPA18	2	2	4	1	2	

	Me-JA		ABA	MBS	LTR	Auxin
	TGACG-motif	CGTCA-motif	ABRE	Drought	Low-temperature	TGA-element
MaEXPA19	1	1	1	1	1	1
MaEXPLA2	3	3	2	2	2	
MaEXPB11	3	3	3			1
MaEXPLB1	1	1		1		
MaEXPLA3	2	2	1	2	1	
MaEXPLB2	1	1	1	2		
MaEXPB12	5	5	5	1		1
MaEXPA20	3	3	3		1	
MaEXPLA4	1	1		1		
MaEXPA21	2	2	1	2	1	1
MaEXPA22	4	4	1	3		2
MaEXPA23	2	2	1	3		1
MaEXPB13	2	2	3		1	1
MaEXPA24	3	3	9		1	
MaEXPA25	2	2	1	1		
MaEXPA26	1	1	6	2		1
MaEXPA27	3	3	2			1
MaEXPA28						
MaEXPA29	3	3	8			1
MaEXPA30	1	1	3			
MaEXPA31	2	2	1			1
MaEXPA32	1	1	7	1		1
MaEXPLB3	1	1	1	1		
MaEXPLA5			1	1	2	1
MaEXPA33	2	2	3		1	
MaEXPA34	2	2	3		2	
MaEXPLA6	4	4	2	1	1	
MaEXPA35	5	5	7			1
MaEXPA36	4	4	2	1		2

Fig. 6 (continued)

additional introns is likely useful in increased gene expression (Jo and Choi 2015).

The evolutionary relationships between *MaEXPs* and *MbEXPs* showed that the subfamily members of both the genome are highly similar at sequence levels as they are grouped as a single cluster. This close relationship among the subgroups can be in feed from the fact that all essential genic regions were present in both A and B genomes (Davey et al. 2013). The high collinearity of the expansins between the A and B genomes in banana indicated that they might have similar functions (Lv et al. 2020). The banana expansin genes clustered with the respective candidate members of rice and *Arabidopsis* suggesting these genes perform the same function as the model plants and might have evolved before the divergence of *Musa* ~ 4.6 Mya (Lescot et al. 2008). Uneven distribution of expansin genes was observed in banana as in the case of many monocots and dicot plants (Zhang et al. 2014; Guimaraes et al. 2017a, b; Li et al 2016a, b). Clustering of genes belonging to the same subfamily, for example, *EXPB* in chr02, suggested that it might be due to tandem and segmental duplication, which lead to major variation in family size and distribution (Cannon et al. 2004; Lv et al. 2020).

The key cis-regulatory elements found in EXP promoters are associated with light and hormonal regulations, notably with response to MeJA. Light responsive promoter motifs are key in determining the molecular changes and biochemical constitutions of multiple biological processes in plants. In addition, previous studies demonstrated that light-response motifs of EXPs are participating in the leaf and shoot growth (Dornbusch et al. 2014; Han et al. 2019). The regulation of EXPs in *Stellaria longipes* was shown to be responsible for shade avoidance (Sasidharan et al. 2008). The presence of cis-elements responsive to hormones suggested that the expression of expansins can be influenced by hormones such as cytokinins (Downes and Crowell 1998), ethylene (Belfield et al. 2005), and auxins (McQueen-Mason et al 1992; Zhao 2012). MeJA and ABRE responsive elements are predominant promoter motifs in EXPs although their interactive relationships in growth and development are yet to be known clearly (Han et al. 2019). The other cis-element related to low-temperature responsive, drought inducibility MBS (CAACTG) and cis-elements related to other abiotic stresses were also present in EXP promoter motifs suggesting their possible role in salt, drought and cold stresses (Chen et al. 2016, 2017; Feng et al. 2019; Ren et al. 2018). Overall, drought-responsive elements were higher in expansin genes of B genome which is known to harbor genes for various abiotic and biotic stresses (Davey et al. 2013). Meristem responsive cis-elements were also present in some of the promoters which confirm its role in leaf and stem initiation and growth (Kuluev et al. 2012; Sampedro et al. 2015).

EXPLA and EXPLB have no paralogues in both the genomes of banana which suggested that these might have occurred recently whereas EXPA and EXPB exist before the divergence of vascular plants (Sampedro et al. 2006). Purifying selection eliminates the deleterious alleles or genetic polymorphism that arises through mutations to maintain the natural fitness of the organism whereas positive selection fixes advantageous mutations and usually leads to species divergence (Yuan et al. 2015). The occurrence of more tandem and segmental duplication in both genomes might be due to negative selection which reveals that this gene family is conserved. Duplication events in *Musa* have occurred recently than the progenitors as a consequence of whole-genome duplication reflecting a conserved and slowly evolving banana expansin gene family (D'Hont et al. 2012) and similar results have been reported for the CCCH-ZFP gene family in banana (Mazumdar et al. 2017). The recent evolution of expansin genes in both the genomes suggested that it is co-evolving with the pathogens (Cosgrove et al. 2015). The occurrence of more paralogues of EXPB in B genome speculated that EXPB is highly evolving and this

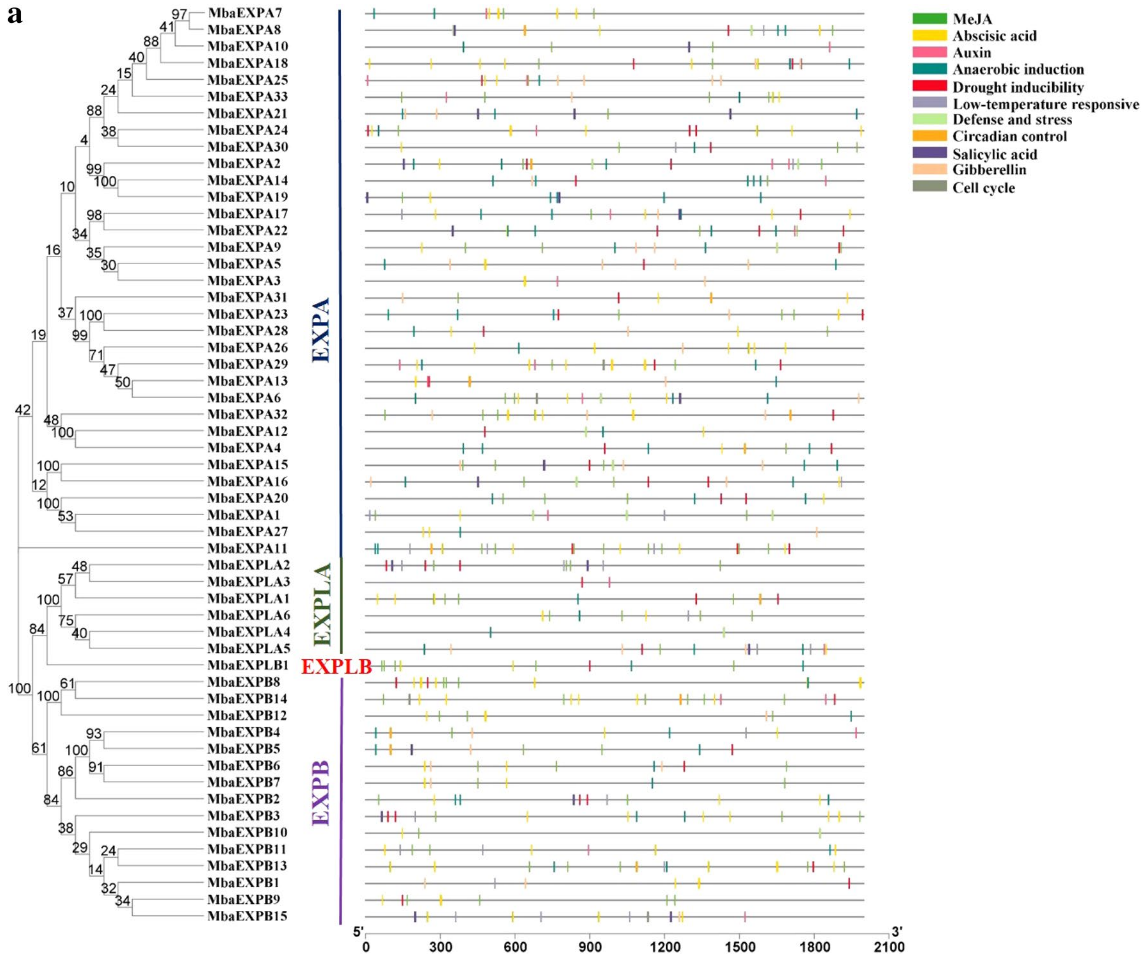
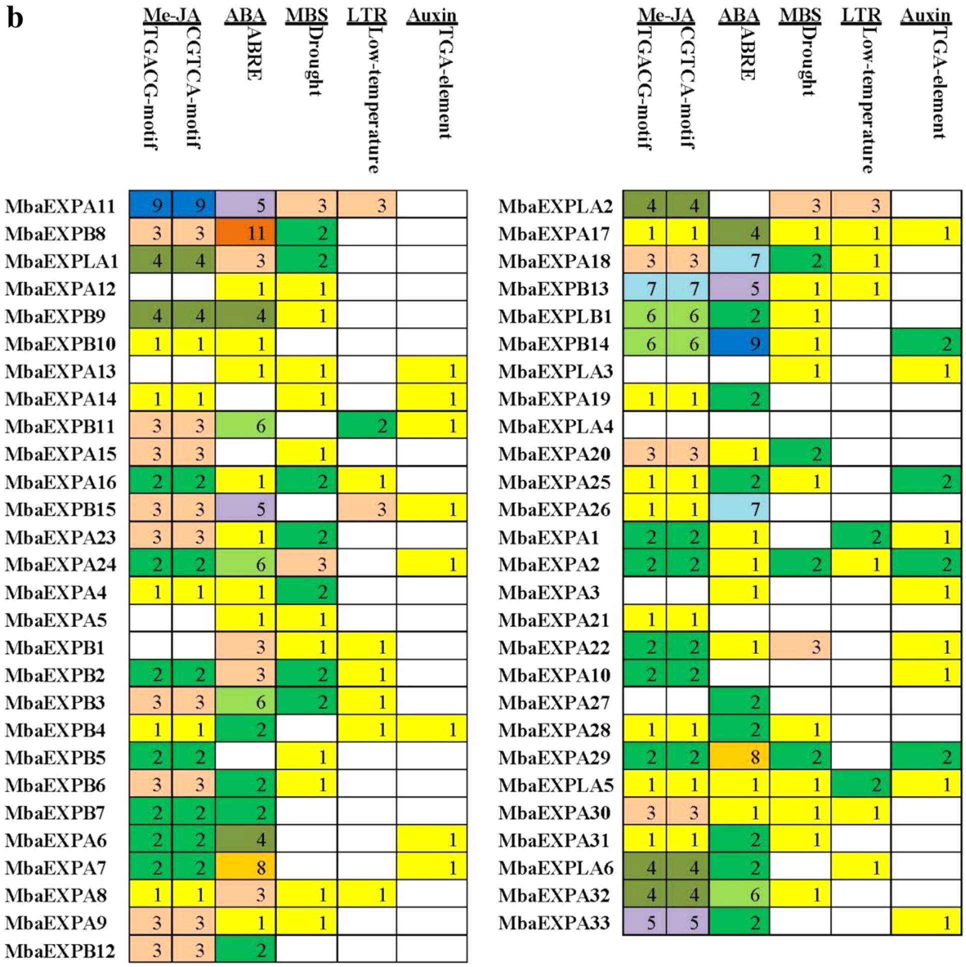


Fig. 7 **a** Predicted cis-elements of expansin gene promotors in Musa B genome. Promoter regions 2000 bp upstream of 55 EXPs analyzed by PlantCARE. Different-colored rectangles represented different cis-elements, and MeJA response elements are highlighted in green ellipses. **b** The number of promoter elements in the MbaEXPs' promoter regions. Five major cis-elements of MbaEXPs are indicated by different-colored boxes with numbers



b

	Me-JA		ABA	MBS	LTR	Auxin
	TGACG-motif	CGTCA-motif	ABRE	Drought	Low-temperature	TGA-element
MbaEXPA11	9	9	5	3	3	
MbaEXPB8	3	3	11	2		
MbaEXPLA1	4	4	3	2		
MbaEXPA12			1	1		
MbaEXPB9	4	4	4	1		
MbaEXPB10	1	1	1			
MbaEXPA13			1	1		1
MbaEXPA14	1	1		1		1
MbaEXPB11	3	3	6		2	1
MbaEXPA15	3	3		1		
MbaEXPA16	2	2	1	2	1	
MbaEXPB15	3	3	5		3	1
MbaEXPA23	3	3	1	2		
MbaEXPA24	2	2	6	3		1
MbaEXPA4	1	1	1	2		
MbaEXPA5			1	1		
MbaEXPB1			3	1	1	
MbaEXPB2	2	2	3	2	1	
MbaEXPB3	3	3	6	2	1	
MbaEXPB4	1	1	2		1	1
MbaEXPB5	2	2		1		
MbaEXPB6	3	3	2	1		
MbaEXPB7	2	2	2			
MbaEXPA6	2	2	4			1
MbaEXPA7	2	2	8			1
MbaEXPA8	1	1	3	1	1	
MbaEXPA9	3	3	1	1		
MbaEXPB12	3	3	2			

	Me-JA		ABA	MBS	LTR	Auxin
	TGACG-motif	CGTCA-motif	ABRE	Drought	Low-temperature	TGA-element
MbaEXPLA2	4	4		3	3	
MbaEXPA17	1	1	4	1	1	1
MbaEXPA18	3	3	7	2	1	
MbaEXPB13	7	7	5	1	1	
MbaEXPLB1	6	6	2	1		
MbaEXPB14	6	6	9	1		2
MbaEXPLA3				1		1
MbaEXPA19	1	1	2			
MbaEXPLA4						
MbaEXPA20	3	3	1	2		
MbaEXPA25	1	1	2	1		2
MbaEXPA26	1	1	7			
MbaEXPA1	2	2	1		2	1
MbaEXPA2	2	2	1	2	1	2
MbaEXPA3			1			1
MbaEXPA21	1	1				
MbaEXPA22	2	2	1	3		1
MbaEXPA10	2	2				1
MbaEXPA27			2			
MbaEXPA28	1	1	2	1		
MbaEXPA29	2	2	8	2		2
MbaEXPLA5	1	1	1	1	2	1
MbaEXPA30	3	3	1	1	1	
MbaEXPA31	1	1	2	1		
MbaEXPLA6	4	4	2		1	
MbaEXPA32	4	4	6	1		
MbaEXPA33	5	5	2			1

Fig. 7 (continued)

may contribute to resistant nature of B genome (Davey et al. 2013). A similar kind of expansion of EXPB subfamily was reported in other monocots such as rice, maize and sugarcane (Santiago et al. 2018). Sampedro et al. (2006) suggested that the divergent EXPB proteins have evolved to substitute xylans such as (glucurono) arabinoxylans which allows more efficient roles in the cell wall mechanics.

Protein–protein interaction network revealed that expansin proteins form functional complexes, mediating the expression of other genes involved in cell wall modification, cell wall structure in root hairs and other root hair specific genes, removal of H_2O_2, oxidation of toxic reductants, biosynthesis, and degradation of lignin and suberization in banana (Lin et al. 2016). Muthusamy et al. (2020) also proved that the overexpression of expansin influences the expression of an interacting gene, the cell wall-plasma membrane linker protein-encoding gene. This suggested that apart from its role in cell wall development and cytoskeleton formation, expansins are also involved in protecting the plant tissues during the stress conditions by preventing oxidative stress which occurred during various biotic and abiotic stress conditions which indicates that expansin has potential of resistance to wide stresses.

Mining the transcriptome profile under specific physiological conditions will facilitate the identification of the best candidate gene/s. Study on the expression of expansin genes in the *Musa* transcriptome data set revealed that the expression of expansins is varying under different stress conditions. In general, the expression pattern of contrasting cultivars is the same except *MaEXPA*18 (− 4.5-fold) and *MaEXPA26* (− 5.3-fold) under drought stress condition. As these genes are significantly downregulated in susceptible cultivar during drought stress, it is speculated that these genes may play a major role in drought tolerance by improving osmotic adjustment (Chen et al. 2016), water retention, and elevating the antioxidant enzymes (Yang et al. 2020). Sampedro and Cosgrove (2005) hypothesized that overexpression of EXPA alter the microtubule arrays, cellulose deposition, and cell wall thickening which are essential for stomatal guard cells and their adjacent cells during

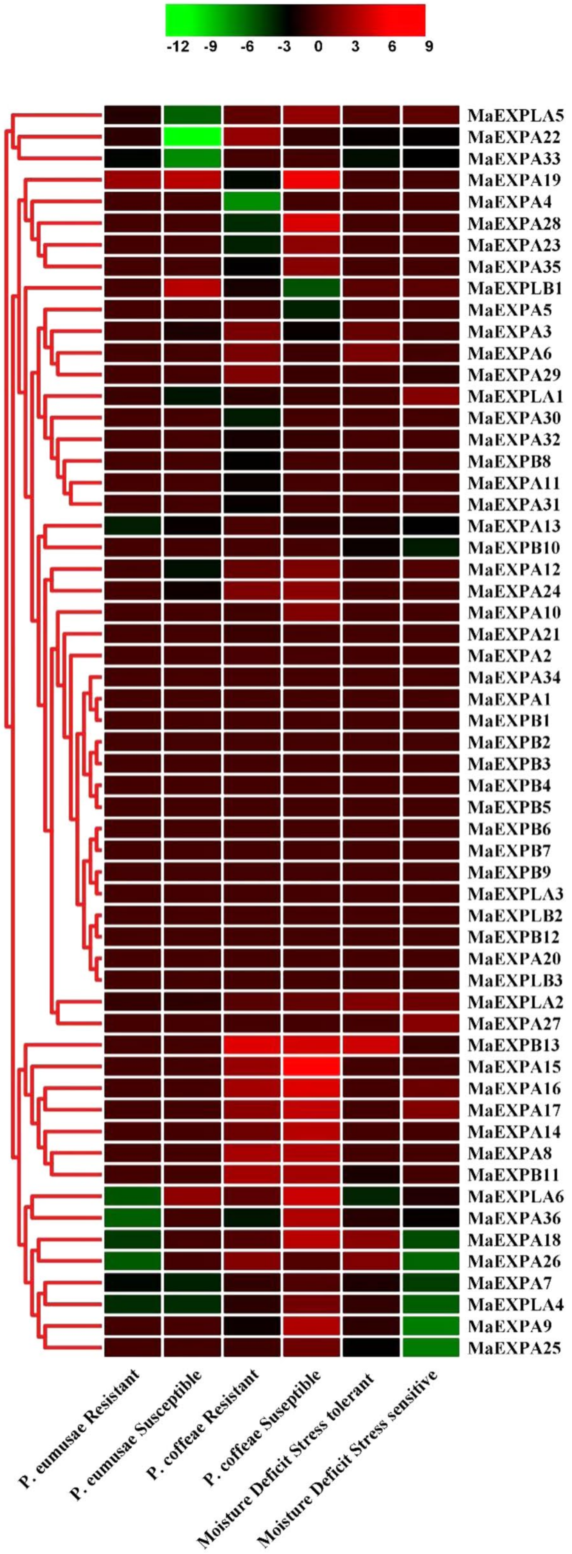


Fig. 8 A graphical representation of expression details of expansin genes in biotic and abiotic stresses in Musa cultivars. The heat map was drawn using log2 logarithmic transformed expression values. Red to green represents high and low expression levels, respectively. Based on the expression, the expansin genes were hierarchically clustered and divided into various gene clusters in the figure

stomatal morphogenesis and thereby enhance the drought tolerance by modifying the leaf growth (Lü et al. 2013). It was observed that *MaEXPB13* is highly upregulated in drought-tolerant cultivar. This is in concordance with the result of Zhang et al. (2019) who reported that significant upregulation of EXPB during drought stress leads to altering the cell walls and thereby reducing the negative effects of drought stress. Li et al. (2011a) and Muthusamy et al. (2020) proved that overexpression of EXPB subfamily induces drought tolerance under water-deficit stage. The presence of cis-elements induced by drought in their promoters again reiterates that the over expression of these expansin genes resulted in drought tolerance. Li et al. (2013) also proved that the efficiency of drought tolerance can be improved by over expression of expansin by manipulating the promoter which driven the expansin gene. Wu et al. (1996) has reported the overall involvement of expansins under drought in various other plant species.

Out of 20 significantly expressed EXP genes, 50% of the genes were downregulated in nematode-resistant cultivar while these genes were either upregulated or no expression variation was observed in the susceptible cultivar upon nematode infection. Upregulation of *EXP* genesin-susceptible cultivar suggested that these genes might act as the susceptible factors as it favors nematodes by loosening the host cell and facilitating easy feeding. A similar kind of upregulation of several expansin genes in syncytia induced by *H. schachtii* in in *A. thaliana* roots was observed by Wieczorek et al. (2006). Cosgrove (2000) also stated that these expansin proteins cause the extension of the cell wall through turgor-driven slippage of cellulose microfibrils in the susceptible cultivar and thereby loosen the cell wall of the host root system which indirectly helps the nematode feeding site. This study suggested that by suppressing the differentially expressed *MaEXPA* genes, the resistance can be improved in susceptible cultivar as it may lead to minimizing the modification and/or restructuring of cell walls in the feeding sites.

A similar kind of expression pattern was observed for all the differentially expressed EXP genes in both the cultivars under Sigatoka stress condition, except for *MaEXPLA*1 and *MaEXPLA*6. But their expression pattern was different in the contrasting cultivar, i.e., *MaEXPLA1* was upregulated and *MaEXPLA6* was downregulated in resistant cultivar. In-depth study on the role of these *EXPLA*s in Sigatoka resistant reaction is warranted. Downregulation of *MaEXPA* and *MaEXPLA* upon *P. eumusae* infection corroborates with the findings of Abuqamar et al. (2013) who proved that absence or downregulation of one of the EXPLA subfamily members led to increased resistance to *Botrytis cinerea*. Chen et al. (2018) reported overexpression of expansin negatively regulates the *Pseudomonas syringae* DC3000 and Tobacco mosaic virus resistance in tobacco. Muthusamy et al. (2020) also

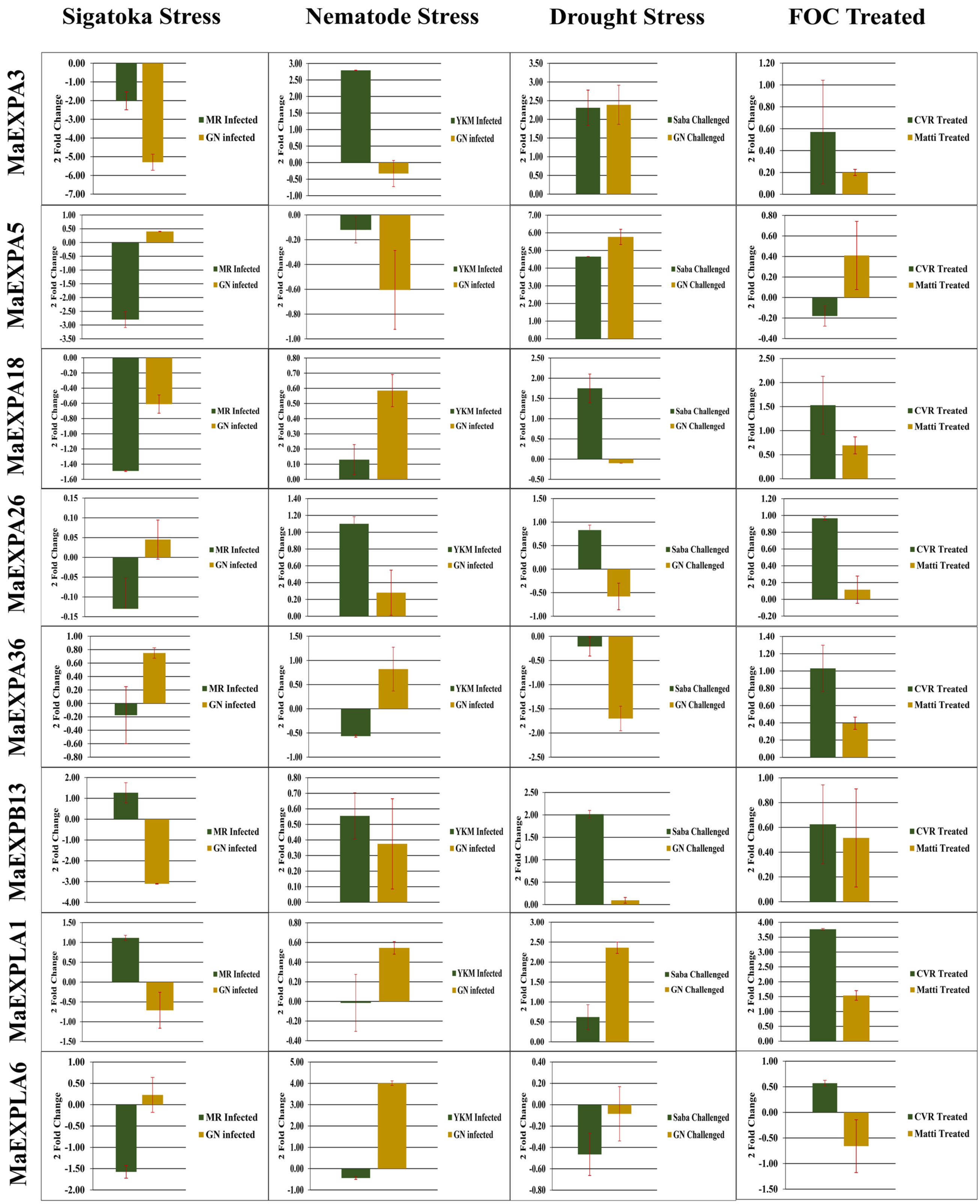
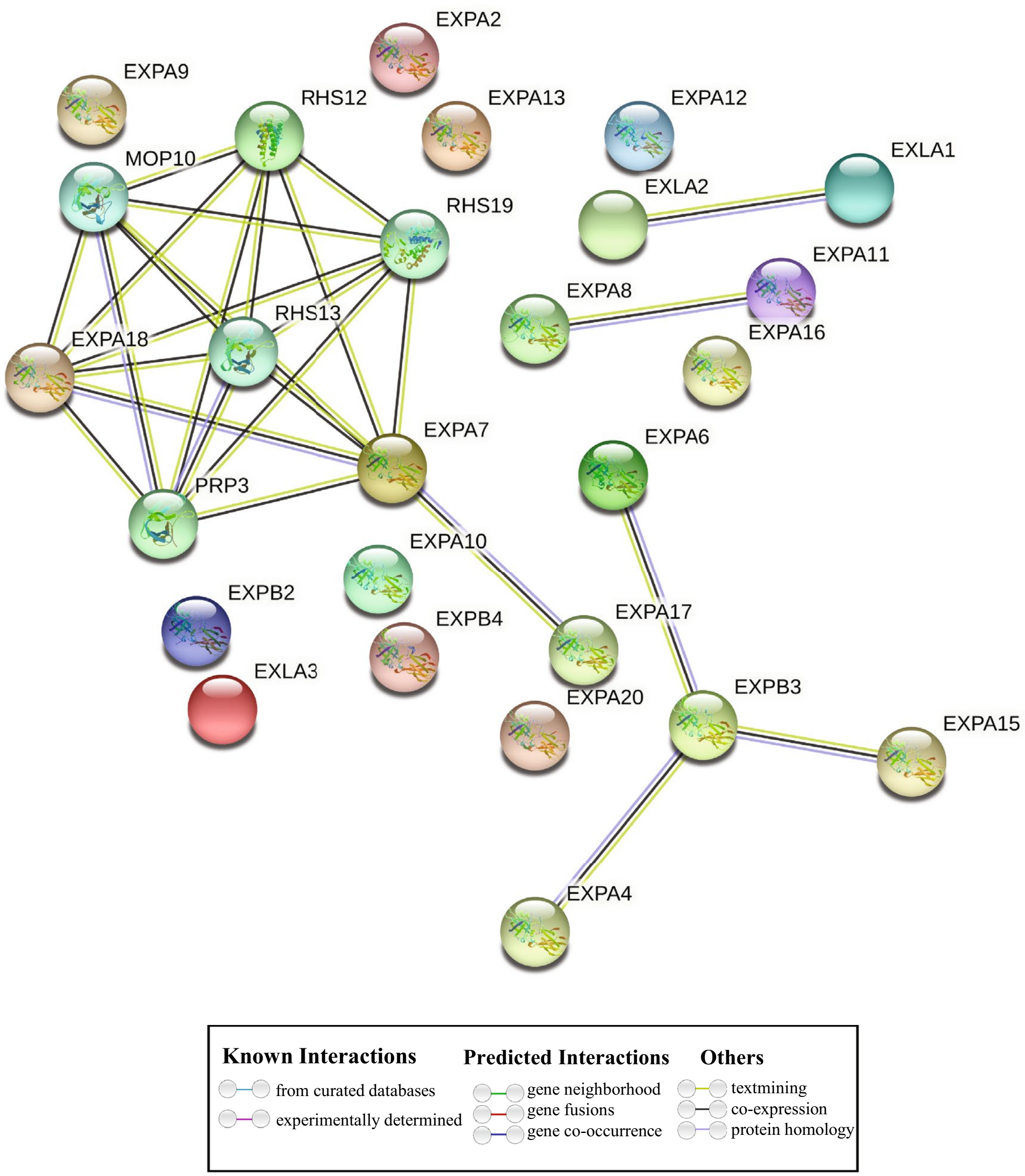
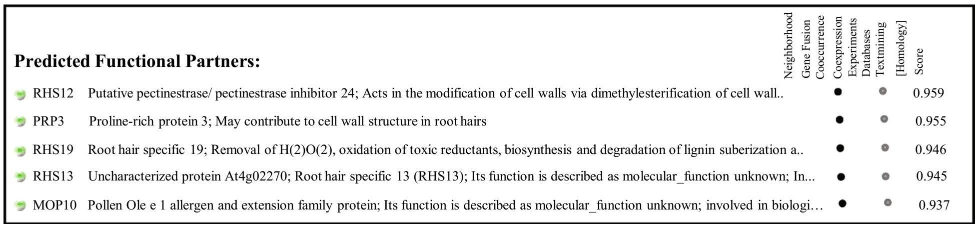


Fig. 9 qRT-PCR expression analysis of eight selected MaEXPs under Sigatoka, Nematode, FOC infected and drought stress samples



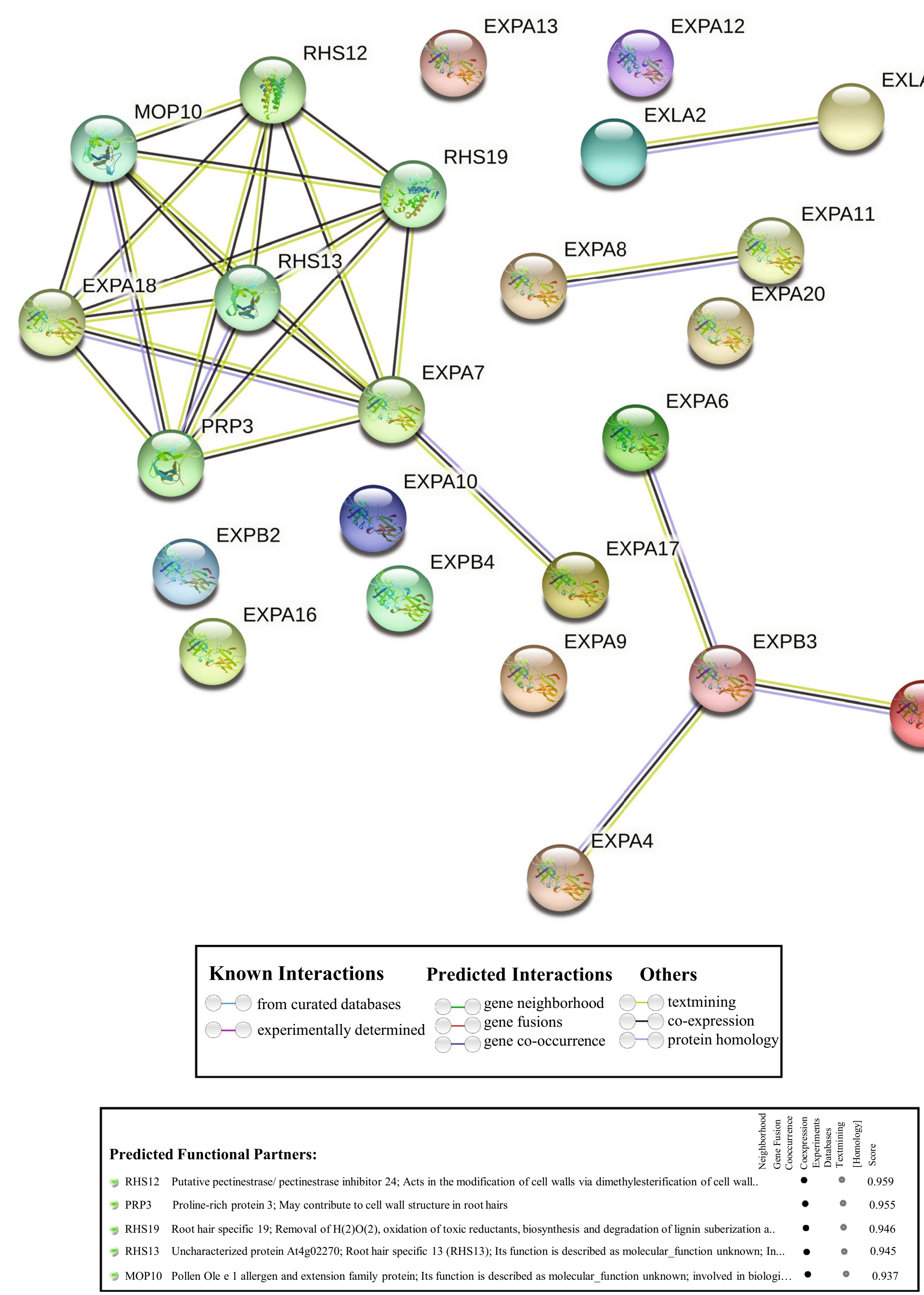


Predicted Functional Partners:

		Neighborhood	Gene Fusion	Cooccurrence	Coexpression	Experiments	Databases	Textmining	[Homology]	Score
RHS12	Putative pectinestrase/ pectinestrase inhibitor 24; Acts in the modification of cell walls via dimethylesterification of cell wall..				●			●		0.959
PRP3	Proline-rich protein 3; May contribute to cell wall structure in root hairs				●			●		0.955
RHS19	Root hair specific 19; Removal of H(2)O(2), oxidation of toxic reductants, biosynthesis and degradation of lignin suberization a..				●			●		0.946
RHS13	Uncharacterized protein At4g02270; Root hair specific 13 (RHS13); Its function is described as molecular_function unknown; In...				●			●		0.945
MOP10	Pollen Ole e 1 allergen and extension family protein; Its function is described as molecular_function unknown; involved in biologi…				●			●		0.937

Fig 10 **a** Protein–protein interaction network of Musa A genome expansin genes with *Arabidopsis thaliana*. **b** Protein–protein interaction network of Musa B genome expansin genes with *Arabidopsis thaliana*

demonstrated that the significant reduction in expression under various biotic stresses such as Turnip mosaic virus, *Pectobacterium carotovorum* and club root diseases alters resistance in *Brassica rapa*. But in-depth study on *MaEXPLA* genes in Sigatoka leaf spot disease resistance



Predicted Functional Partners:

		Neighborhood	Gene Fusion	Cooccurrence	Coexpression	Experiments	Databases	Textmining	[Homology]	Score
RHS12	Putative pectinestrase/ pectinestrase inhibitor 24; Acts in the modification of cell walls via dimethylesterification of cell wall..				●			●		0.959
PRP3	Proline-rich protein 3; May contribute to cell wall structure in root hairs				●			●		0.955
RHS19	Root hair specific 19; Removal of H(2)O(2), oxidation of toxic reductants, biosynthesis and degradation of lignin suberization a..				●			●		0.946
RHS13	Uncharacterized protein At4g02270; Root hair specific 13 (RHS13); Its function is described as molecular_function unknown; In...				●			●		0.945
MOP10	Pollen Ole e 1 allergen and extension family protein; Its function is described as molecular_function unknown; involved in biologi...				●			●		0.937

Fig 10 (continued)

is obligatory to understand their contribution to various resistant reactions.

Conclusion

Genome-wide analysis of the expansin gene family was performed in A and B genome of banana and its expression under various biotic and abiotic stresses were studied. Our finding provides new insight into the structure, evolution, divergence, and function of banana expansins. The RNA-seq data revealed that the expression pattern of expansin genes is varied for biotic and abiotic stresses. The differential expression pattern of *MaEXPA18* and *MaEXPA*26 in the contrasting cultivars for drought stress revealed that these might be candidate genes for drought-tolerant mechanisms. Differential expression of *EXPA* gene members among the *P. coffeae*-resistant (down) and -susceptible (up) cultivars emphasized their role in nematode-resistant reaction. The downregulation of MaEXPLA6 in *P. eumusae*-resistant cultivar under challenged condition reiterate their involvement in resistant mechanism. Further in-depth study on members of these expansin subfamilies will pave way for confirming their candidature for stress resistance in bananas.

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Author contributions Conceptualization, resources, writing, and overall monitoring: SBR. Draft preparation, review and editing: CA. Sample preparation and analysis: RT, PG, and MM. Methodology, in silico analysis, work design, and formatting: ACS. qRT-PCR work and data analysis: BR and PSK. Supervision, conceptualization, and project administration: SU.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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